

NEW ACTINOPTERYGIAN FISH FROM THE NAMURIAN MANSE BURN FORMATION OF BEARSDEN, SCOTLAND

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ABSTRACT. Four new species of actinopterygians are described from the Manse Burn Formation (Namurian) of Bearsden, Glasgow, Scotland. Two fusiform species are members of, and a third is questionably assigned to, *Mesopoma*: *M. carricki*, *M. ? smithsoni*, and *M. pancheni*. A new gibbose species is assigned to a new genus, *Frederichthys musadentatus*. *Mesopoma* is reviewed and rediagnosed, and its relationships to *Frederichthys* are examined with regard to a recent analysis of early actinopterygian (palaeoniscid) phylogeny; *Mesopoma* is a member of a probably paraphyletic group within a polytomous stem-group actinopteran radiation. An alternative phylogeny places *Mesopoma* on the common stem-group of the Haplolepididae, Aeduellidae, and Redfieldiformes. *Frederichthys* is closely related to the platysomids. Otoliths preserved within the mesopomid material are described and compared with those of other osteichthyans; the presence of three pairs of otoliths as a teleostome characteristic is questioned.

THE Bearsden site was discovered and excavated by Mr S. P. Wood (Wood 1982), with the assistance of the Hunterian Museum, University of Glasgow, and the Nature Conservancy Council, during the summers of 1981 and 1982. The fauna includes a diverse assemblage of early actinopterygians, from small, fusiform species of *Mesopoma* to large, rhombic-bodied species of *Amphicentrum* (Traquair 1879; Wood 1982; Coates 1988), a wide variety of crustaceans (Clark 1990, 1991), and remarkably well-preserved chondrichthyans (Dick *et al.* 1986). The closest comparable faunas are those of Bear Gulch, Montana (Lowney 1980, 1985; Lund and Melton 1982), which is also Lower Namurian, and Glencartholm (Dumfries and Galloway) of the Upper Viséan (Traquair 1881; Moy-Thomas and Bradley Dyne 1938). However, these three faunas have very little taxonomic overlap.

Early actinopterygian classification is currently undergoing a major review. Gardiner and Schaeffer (1989) produced a provisional scheme in which they incorporated a wide range of Palaeozoic taxa into groups regarded tentatively as monophyletic. The present paper is not intended to be an exhaustive review of their analysis, and no alternative hypothesis of interrelationships is provided. This problem will be addressed only after the publication of the Bearsden actinopterygians has been completed. The three new species of *Mesopoma*, and the species of *Frederichthys* gen. nov., are described and incorporated into Gardiner and Schaeffer's cladogram, with limited discussion of the relevant synapomorphies and resultant taxonomic positions.

Institutional abbreviations used in this work are: BM(NH), Natural History Museum, London; NMS, National Museum of Scotland, Edinburgh; GLAHM, Hunterian Museum, University of Glasgow; GN, University Museum of Zoology, Cambridge; SPW, the collection of Mr S. P. Wood, Edinburgh.

LOCALITY AND HORIZON

The Bearsden site is located near Glasgow, Scotland. The type locality for the Manse Burn Formation is the Manse Burn, near Bearsden (Ordnance Survey Grid reference NS 529427329 – NS 53057325) (Clark 1989). The Manse Burn Formation has been dated as Pendleian (Namurian) E₁ Zone, based upon spore, conodont, and goniatic analysis. Clark defined the Formation as

including the shales from the Top Hosie Limestone Marine Band to the base of the first thick sandstone. The Formation has been subdivided into six members on the basis of the fossil content and sedimentological characteristics of the shales: the Shrimp member, the Posidonia Member, the Nodular Shale Member, the Platey Shale Member, the Betwixt Member, and the Lingular Member. These Members correspond approximately to the 'beds' presented by Wood (1982). The fossil fish, and an abundance of crustaceans, are contained in finely laminated shales of the Shrimp Member, which has now been identified at several other localities in the western Midland Valley of Scotland (Clark 1989). The shales of the Manse Burn Formation are considered to have been deposited during conditions of varying salinity and oxygenation. The Shrimp Member bears evidence of a sequentially marine and non-marine environment, subject to seasonal fluctuations.

SYSTEMATIC PALAEOLOGY

Class ACTINOPTERYGII Woodward, 1891

Infraclass ACTINOPTERI Cope, 1871

Genus MESOPOMA Traquair, 1890

Type species. Canobius pulchellus Traquair, 1881, from the Glencartholm Volcanic Beds (C₂/5, Zone, Viséan) of Glencartholm, Dumfries District, Scotland.

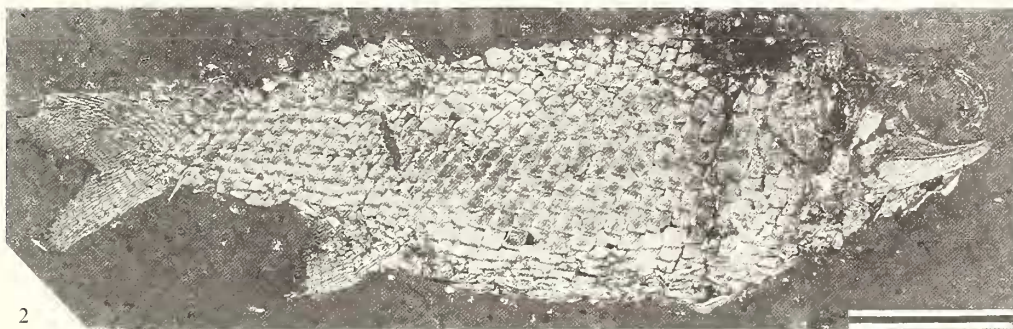
Emended diagnosis. Scales arranged in 30–40 vertically oriented sigmoid rows; all fins bearing fringing fulcra; pelvic fin insertion narrow; pectoral fin rays proximally unjointed; anteroposteriorly narrow post-temporal; branchiostegal series reduced; surangular present; postorbital region of maxilla reduced, jaw articulation sited anteriorly relative to parietal-extrascapular suture; marginal dentition consisting of short uniformly sized conical teeth; dermohyal short; preopercular with short anterodorsal limb; posterior infraorbital narrow; parietals short and almost equilateral; frontals long, projecting into embayed rear of median rostral; nasals narrow; dermopterotic short; dermosphenotic triradiate and contacts nasal; hyomandibula with opercular process; ceratohyal bar consisting of two ossifications.

Included species. *M. pulchellum*, *M. politum*, *M. macrocephalum*, *M. crassum*, *M. ardrossense*, *M. becketense*, *M. carricki*, *M. pancheni*, and *M. ? smithsoni*.

Remarks. *Mesopoma* was erected by Traquair (1890) to separate from *Canobius* Traquair, the species *pulchellus* and *politus*, and from *Rhadinichthys* Traquair, the species *macrocephalus*. These three species were considered to have a configuration of dermal skull bones which placed them between the apparently advanced form of *Canobius* and the more 'typically palaeoniscid' (Traquair 1890) pattern of *Rhadinichthys*. However, Woodward (1891) placed all three species in *Canobius*, considering the erection of a new genus for these species to be premature, because they were insufficiently known. Traquair (1912) withdrew *Mesopoma*, because of difficulty in constructing an

EXPLANATION OF PLATE I

- Fig. 1. *Mesopoma carricki* sp. nov.; NMS 1981.63.54b; latex peel of specimen, showing dermal ornament and isolated pores in (split) rostral region. Scale bar = 5 mm.
- Fig. 2. *Mesopoma carricki* sp. nov.; GLAHM V8254; sealed with cellulose and photographed under toluene; note apparent patterning of squamation. Scale bar = 10 mm.
- Fig. 3. *Frederichthys musadentatus* gen. and sp. nov.; composite photograph of specimens GLAHM V8286a–b immersed in toluene; for line drawing of specimen, see Text-fig. 9. Scale bar = 10 mm. Photographs for figs 2–3 taken by Dr J. K. Ingham; reprinted with permission of the Hunterian Museum, University of Glasgow.



adequate diagnosis. All three species were again placed in *Canobius*, with the addition of a new species, *Canobius crassus* Traquair, 1914. *Mesopoma* was resurrected by Moy-Thomas and Bradley Dyne (1938) in their description of the Glencartholm actinopterygian fauna. They provided a new generic diagnosis, and new descriptions of *M. pulchellum*, *M. politum*, and *M. crassum*. Moy-Thomas (1938) published a further diagnosis of *Mesopoma*, together with a redescription of *M. macrocephalum*, and a description of another new species, *M. ardressense*. Lowney (1980) has also rediagnosed *Mesopoma*, and described another new species, '*M. becketense*', from Bear Gulch, Montana. Most recently, Gardiner and Schaeffer (1989) have characterized a '*Mesopoma* group', which is incorporated within their reclassification of lower actinopterygian fishes.

No type species for *Mesopoma* has been formally proposed; this role must therefore be assigned to *M. pulchellum* under the 'first species rule' (article 69, recommendations 69B (9) & (10), International Code of Zoological Nomenclature 1985).

Mesopoma carricki sp. nov.

Plate 1, figs 1–2; Text-figs 1–3

Derivation of name. The species is named after the late James A. Carrick, formerly of the Hunterian Museum, University of Glasgow, who helped significantly at the Bearsden excavation in 1982.

Holotype. GLAHM V8289a–b.

Referred specimens. The above mentioned holotype, together with NMS 1981.63.44; NMS 1981.63.46; NMS 1981.63.47; NMS 1981.63.53; NMS 1981.63.54a–b; NMS 1981.63.55a–b; NMS 1987.7.131; GLAMH V8254; BM (NH) P62370; BM (NH) P62372a–c; SPW 2294a–b; SPW 2282; SPW 2285a–c.

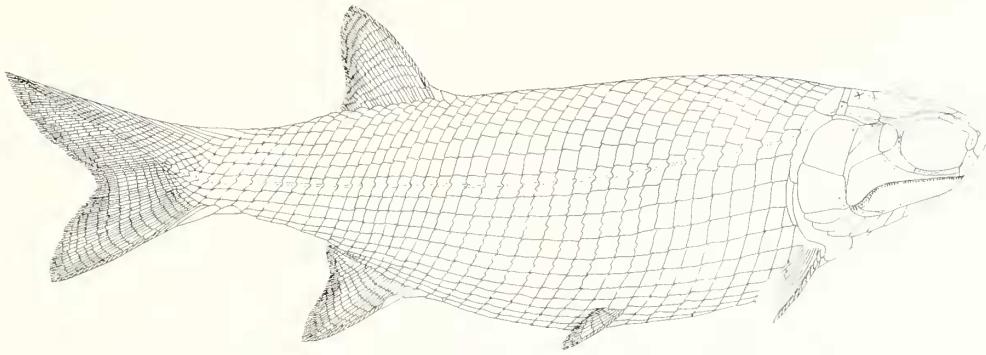
Horizon and locality. Shrimp member, Manse Burn Formation, Pendleian (Namurian) E₁ Zone, Lower Carboniferous, Bearsden, Glasgow, Scotland.

Diagnosis. Bulbous rostral and other dermal skull bones pierced occasionally by large pores not associated directly with the sensory canal system; single ovoid suborbital; dermohyal short and triangular; opercular five-sided; six branchiostegal rays; all median fins preceded by three basal fulcra; posterior basal fulcral scale preceding anal fin with narrow mid-region; squamation arranged in thirty eight rows; largest scales in flank region with serrated posterior edge; scales devoid of ornament except for two or three grooves parallel to anterior edge; maximum of seven scales above and ten below lateral line.

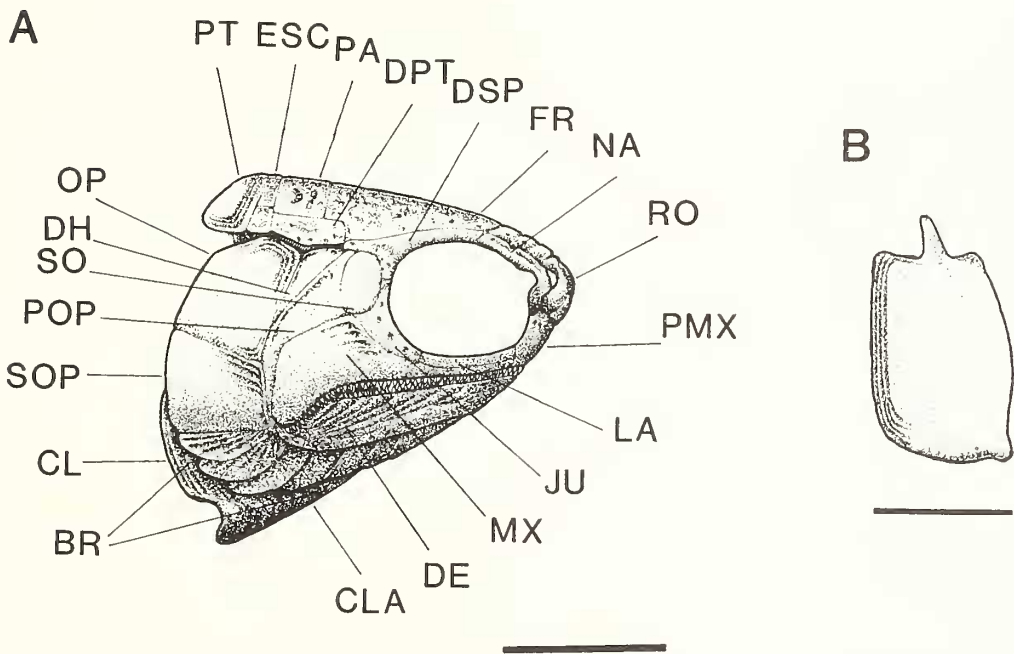
Discussion. *M. carricki* may be distinguished from *M. pancheni* on the basis of the following characters: a V-shaped rostronasal: frontal suture; isolated pores piercing dermal skull bones; the pattern of rostral ornament; the lack of highly ornamented scales behind the post-temporals; scales with mostly smooth surface, fewer anterior grooves, and scale proportions (compare Text-figs 2 and 6).

Description. This is one of the most frequently found actinopterygian species at the Bearsden site. *M. carricki* has been restored as a compressed fusiform fish (Keast and Webb 1966) because most articulated specimens are preserved lying on one side. The head is short relative to most other Palaeozoic fusiform actinopterygians, with a large orbit and near vertical jaw suspension. The skull, measured from the rostral apex to the rear of the operculogular series, is c. 12.5 mm long; the total body may reach 70 mm in length (Text-fig. 1).

Skull and lower jaw. Details of the skull are most clearly preserved in specimens GLAHM V8289 (Text-fig. 3) and NMS 1981-63-54b (Pl. 1, fig. 1). The maxilla is short, with a subrectangular posterior expansion (Text-figs 1, 2A, 3). A series of two or more small pits lies adjacent to the jugal border; the dermal ornament is restricted to the anterodorsal region. The maxilla bears a single row of uniformly sized small conical teeth. The preopercular has a slender vertical stem and a short anterodorsal limb; the sensory canal lies next to the posterodorsal edge. The short, triangular dermohyal is pierced by a single pit (Text-figs 1, 2A). An ovoid



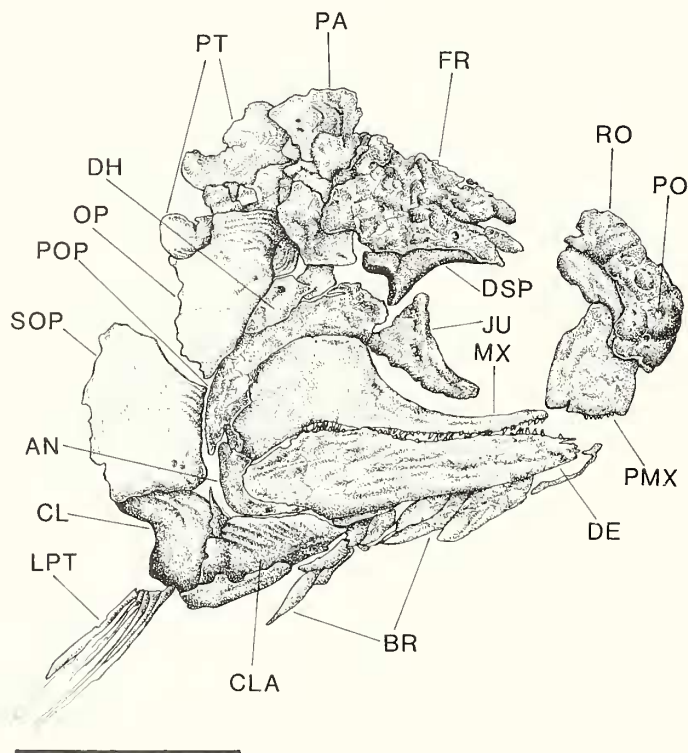
TEXT-FIG. 1. *Mesopoma carricki* sp. nov., restoration. Scale bar = 10 mm.



TEXT-FIG. 2. *Mesopoma carricki* sp. nov. A, restoration of dermal skull showing ornament. Scale bar = 5 mm. B, anterior flank scale. Scale bar = 1 mm. Abbreviations: AN, angular; AR, articular; ASP, ascending process of parasphenoid; BH, site of buccohypophyseal foramen; BPT, basiptyergoid process; BR, branchiostegal ray(s); CL, cleithrum; CLA, clavicle; DE, dentary; DH, dermohyal; DSP, dermosphenotic; ESC, extrascapular; FMC, foramen for mandibular sensory canal; FR, frontal; GF, glenoid fossa; GL, lateral gular; HPLA, horizontal lamina of prearticular; JU, posterior infraorbital; LA, anterior infraorbital; LPT, lepidotrichia; MX, maxilla; NA, nasal; OP, opercular; PA, parietal; PAR, prearticular; PCL, postcleithrum; PMX, premaxilla; PO, pore not associated with sensory canal; POP, preopercular; PT, post-temporal; RO, rostral; SCL, supracleithrum; SO, suborbital; SOP, subopercular; ST, supratemporal; TS, tooth sockets.

suborbital lies between the preopercular and the infraorbital series (Text-fig. 2A). The triradiate dermosphenotic carries the otic portion of the infraorbital canal through posterior and ventral rami into the crescentic posterior infraorbital. Four pores overlie the sensory canal, which passes into a slender, tubular anterior infraorbital; neither bone is ornamented. The skull table bears anastomosing flattened tubercles and ridges (Plate I, fig. 1). Four extrascapulars carry the occipital commissure. A short dermopterotic with a convex lateral edge encloses

the otic portion of the infraorbital canal. The anterodorsal angle of the dermopterotic fits into the embayed posterolateral corner of the frontal. The subequilateral parietals have strongly convex anterior edges. The frontals are more than twice the length of the parietals; the supraorbital canal exits anterolaterally to join the nasal. The united anterior frontal apices project into the embayed posterodorsal rostral edge. Large crystalline otoliths are preserved occasionally beneath the dermopterotic. All examined specimens are in poor condition (surface detail has been lost); each is pear-shaped with the longest axis almost equal to the length of the dermopterotic (2.6 mm). The lateral surface is flat and the mesial surface slightly convex. Only one otolith has been found on each side of the skull. The large, characteristically bulbous, rostral resembles those of *Rhadinichthys canobiensis*, var. *elegantulus* Traquair, *Rhadinichthys planti* Traquair, and *Mesopoma pancheni* sp. nov. (Text-figs 2A,3). The bilaterally symmetrical ornament of broad ridges and tubercles is illustrated in Text-figure 3 and Plate 1, figure 1. Pores pock-mark the posterodorsal region (NMS 1981.63.54*b*) resembling those described in the snout of *Mimia toombsi* Gardiner (1984; interpreted as containing twigs of the upper branch of the profundus nerve (V)). The convex ventral edge overlaps the dorsomedial region of the premaxillae; whether it contains the ethmoid commissure is unclear. Long, narrow nasals flank the rostral; a groove next to the anterior edge marks the course of the supraorbital canal. Tall, smooth, subrectangular premaxillae contribute to the anteroventral orbital rim, and bear small conical teeth. The ethmoid commissure passes towards the ventral region of the rostral. The ethmoidal osteological pattern resembles closely that of the Gogo actinopterygians (Gardiner 1984), in which the commissure enters the rostral. The correspondent identification of the derm-ethmoidal shield of *Mesopoma* as consisting of a rostral and premaxillae, rather than a post-rostral and rostro(antorbito-)premaxillae (with implicit hypotheses of bone fusion) appears to be the most parsimonious interpretation. The palate is known from fragments of pterygoid material, covered with small granular teeth. The lower jaw consists of a large dentary, a slender angular, and a surangular. The dentary is ornamented with bifurcating grooves, which radiate from the posteroventral corner. The dentition consists of numerous small conical teeth, all of approximately uniform size and lying in a single row. The irregularly pentagonal opercular is taller and narrower than the subopercular. Two or three shallow grooves



TEXT-FIG. 3. *Mesopoma carricki* sp. nov., GLAHM V8289*a*, holotype. Abbreviations: see Text-figure 2. Scale bar = 5 mm.

ornament the surface adjacent to the anterodorsal corner, occasionally pierced by an isolated pit (obscured by the right parietal in Text-figure 3). The subopercular is trapezoid, with a slightly convex posterior edge; four or more shallow grooves score the anterodorsal quarter of the surface, and two further pits lie in the anteroventral corner. The branchiostegal series consists of six rays which become narrower anteriorly, and an elongate triangular gular.

Pectoral girdle. The post-temporal is anteroposteriorly narrow, with an expanded posteroventral region (Text-figs 1–3). The lateral line canal passes through the anteroventral corner. The posterior edge of the ovoid supracleithrum bears four or more widely spaced serrations. The sensory canal traverses the dorsal, broadest, region. The cleithrum has a robust vertical blade, with an acute median angle dividing the post-branchial lamina from the posterolateral region. Apices of the ridged dermal ornament appear to be slightly denticulated. The elongate postcleithrum has a gently convex posterior edge. Fragments of the clavicle appear to be ornamented similarly to the cleithrum. The interclavicle is unknown.

Fins. All fins bear fringing fulcra. The dorsal and anal fins are situated opposite each other in the rear half of the body (Text-fig. 1). The subtriangular dorsal fin has a convex leading edge. The fin consists of twenty five or more lepidotrichia which articulate at even intervals throughout their length, and bifurcate distally before reaching the slightly emarginated trailing edge. The anal fin is similar to the dorsal fin, although more acuminate. The caudal fin consists of sixty or more lepidotrichia which are articulated throughout their length and bifurcate distally. The heterocercal tail has a deeply cleft, almost symmetrical profile. The incomplete pectoral fins consist of eight or more proximally unjointed lepidotrichia. The leading edge includes at least one primary, unbifurcated lepidotrich. The pelvic fin is small, subtriangular, and narrow based; situated about halfway between the anal fin and the pectoral girdle. It consists of ten or more articulated, distally bifurcated lepidotrichia.

Squamation. The most complete squamation is preserved in specimen GLAHM V8283; Plate 1, figure 2, shows dark bands within the scales, visible when the specimen is immersed in a solvent. The emergent pattern may be specifically diagnostic, but whether it preserves the patterning of the fish when alive, or merely the distribution of some other feature (e.g. ganoine density), remains uncertain. The large, rhomboidal scales have a clearly defined anterodorsal process (Text-fig. 2B). The trunk, from the origin of the tail to the rear of the pectoral girdle, bears thirty eight almost vertically oriented rows (Text-fig. 1). Mid-flank scales have a gently serrated posterior edge. The caudal lobe is not steeply up-turned; intercalary scale rows are inserted ventrally at the base of the tail. A maximum of seven scales lie above, and ten below, the lateral line. A pair of fine grooves run parallel to the anterior and dorsal scale edges which may represent growth lines or restricted dermal ornament. A cut-water of fulcral scales lies along the dorsal mid-line of the caudal lobe. The insertions of the caudal, dorsal, and anal fins are each preceded by three basal fulcra. Specimen NMS 1981.63.53 has an unusual, waisted fulcral scale preceding the anal fin.

Mesopoma? smithsoni sp. nov.

Text-figs 4–5

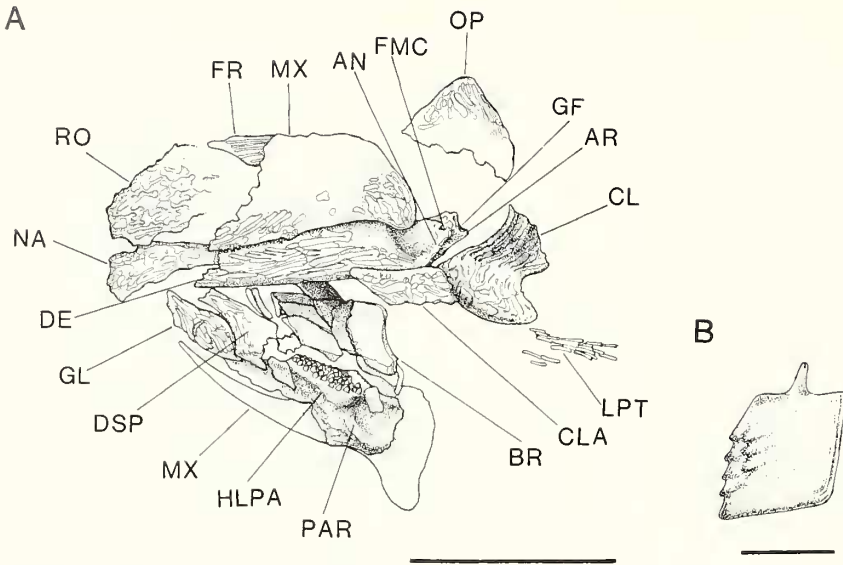
Derivation of name. Named after Dr T. R. Smithson, who provided valuable discussion and advice throughout the course of research on the Bearsden actinopterygian material.

Holotype. NMS 1981.63.43a–b.

Referred specimens. NMS 1981.63.31; NMS 1981.63.40a–b; NMS 1987.7.129a–b; GLAHM V8290a–b; GN 1022a–b; GN 1064; BM (NH) P62373a–b; SPW 2001a–b; SPW 2003a–b; SPW 2004; SPW 2007; SPW 2288; SPW 2292a–b; SPW 2295a–b.

Horizon and locality. Shrimp member, Manse Burn Formation, Pendleian (Namurian) E₁ Zone, Lower Carboniferous, Bearsden, Glasgow, Scotland.

Diagnosis. Postorbital region of maxilla accounts for less than half of its total length; lower jaw with greatly thickened prearticular bearing numerous large, rounded, flattened teeth; opercular rectangular with rounded posterodorsal corner; subopercular with extended anteroventral corner; gulars large with single curved pit-line; squamation arranged in thirty two or more rows; scales in flank region with faint, oblique, ridged dermal ornament; squamation approaching post-temporals



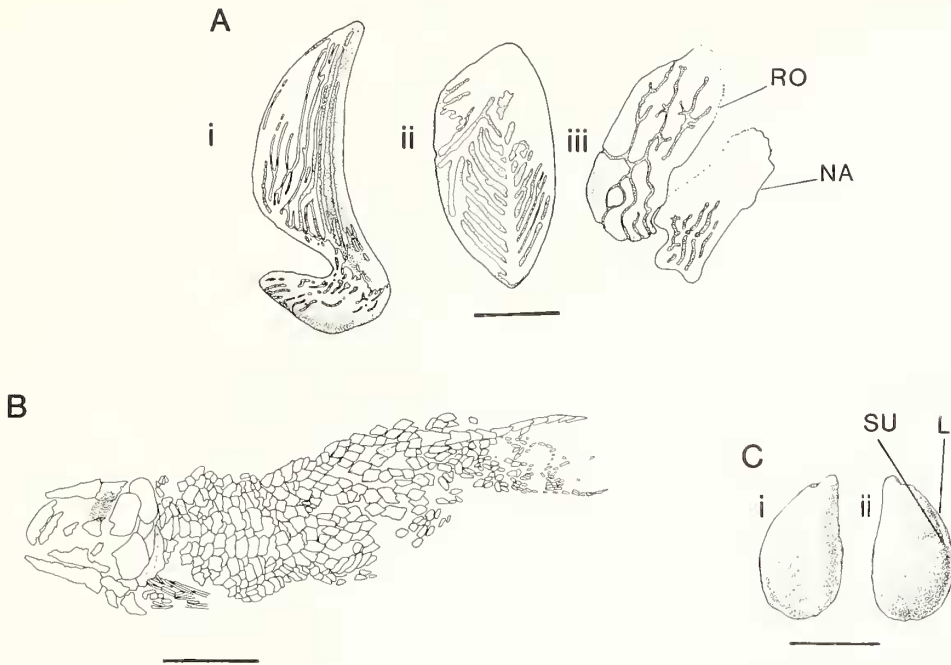
TEXT-FIG. 4. *Mesopoma? smithsoni* sp. nov. A, GN 1064. Disarticulated skull and pectoral girdle showing incomplete jaws with thickened prearticular. Scale bar = 10 mm. B, anterior flank scale. Scale bar = 1 mm. Abbreviations: see Text-figure 2.

has most pronounced ornament and convex posterior edges; eight or more scales above and eight or more below lateral line.

Discussion. *M.? smithsoni* is questionably assigned to *Mesopoma* on the basis of the following characters: the short postorbital region of the maxilla; uniformly sized, small marginal teeth; short parietals and long frontals; post-temporal anteroposteriorly narrow; squamation arranged in thirty two or more, vertically oriented sigmoid rows. *M.? smithsoni* most closely resembles *M. crassum*, sharing similar gross proportions, dermal ornament, and maxillae, but can be distinguished from the latter by the presence of specialized buccal dentition, a much broader opercular and the absence of a continuous line of ridge scales from the post-temporals to the dorsal fin insertion.

Description. This is the largest and most robustly constructed of the three species of *Mesopoma* found in the Bearsden fauna. Individual fish may be up to 80 mm long, an estimate based upon the most complete specimens of an incompletely known species.

Skull and lower jaw. The subrectangular postorbital region of the maxilla is more angular than that of *M. carricki*, accounts for less than half of the total length, and bears uniformly small teeth (Text-fig. 4A). Dermal ornament is limited to patches of broad tubercles and ridges originating at the ventral margin. The preopercular, quadratojugal, dermohyal, suborbital and infraorbitals appear to be similar to those of the larger members of this genus (cf. *M. crassum* Traquair, Moy-Thomas and Bradley Dyne 1938; Text-fig. 12G). The anteriorly slender dermosphenotic expands posteriorly, towards what may have been a T-junction as found in *M. carricki*. This and a slender anterior infraorbital are ornamented with discontinuous ganoine ridges and tubercles. Anteriorly convex, equilateral parietals project into the embayed posterior edge of the long frontals. The skull table bears irregularly shaped, flattened ganoine ridges. A single otolith is preserved on each side of the skull in several specimens (Text-fig. 5ci and 5cii depict the left otolith of GN 1022). The laterally compressed, pear-shaped otoliths consist of a crystalline material which reacts vigorously with a 10 per cent solution of acetic acid; therefore thought to be calcitic rather than phosphatic. An elongate, narrow sulcus borders the mesial surface of the convex posterior edge. The sulcus may extend around the posteroventral region, contributing to the delineation of a narrow crest along the posteroventral and anteroventral edge. The mesial surface is strongly convex; the less convex lateral surface has a shallow central depression from which



TEXT-FIG. 5. *Mesopoma? smithsoni* sp. nov. Ai, cleithrum; Aii, supracleithrum; Aiii, incomplete rostral and nasal; all from specimen NMS 1981.63.43a. Scale bar = 2 mm. B, almost complete squamation of specimen GN 1022a in lateral view; stippled area indicates site occupied by otolith. Scale bar = 10 mm. C, left otolith from specimen GN 1022a: i, lateral surface; ii, mesial surface. Scale bar = 2 mm. Abbreviations: L, lip; SU, sulcus; for others, see Text-figure 2.

faint grooves radiate posteroventrally. No growth-lines are apparent. The skull table and broad rostral are ornamentally similar (Text-figs 4A, 5Aiii). The nasal ornament resolves into more longitudinally oriented ridges; there is no distinct notch for the posterior nostril. The edges of the lower jaw bones are indiscernible. A smooth surangular area is surrounded by a thick ornament of ganoine ridges. The slender angular is pierced dorsally by a foramen for the mandibular sensory canal (FMC, Text-fig. 4A). The articular (AR) and glenoid fossa (GF) are visible in specimen GN 1064 (Text-fig. 4A). It is unclear whether the glenoid consists of more than a single articular depression. The thickened prearticular (PAR, Text-fig. 4A) has a pronounced angle dividing the smooth ventromesial surface from a broad dorsal lamina (HLP, Text-fig. 4A), which bears large, rounded and flattened subconical teeth. The prearticular cannot be distinguished from coronoidal material. The subrectangular opercular is ornamented with a few broad flattened ganoine ridges which arise from the rounded anterodorsal corner; most of the external surface is smooth (OP, Text-fig. 4A). The similarly patterned subopercular is slightly smaller with an extended anteroventral corner. Fragmented remains of the branchiostegal plates resemble those of *M. carricki*. A pair of gular plates is incompletely preserved in a few specimens, including GN 1064 (GL, Text-fig. 4A). A crescentic pit line lies in the central; the dermal ornament consists of further closely packed short ganoine ridges.

Pectoral girdle. The post-temporals, notably from NMS 1981.63.43a-b, appear to be narrow anteroposteriorly. The short, elliptical, supracleithrum is ornamented with thick enamel ridges (Text-fig. 5Aii). The lateral line canal traverses the broadest span, and exits in front of the dorsal apex. The robust cleithrum has a tall, bipartite vertical blade (Text-fig. 5Ai) with a denticular-crested dorsal ornament (cf. *Amia* Jarvik 1980). The moderately-sized clavicle has a smooth anterolateral margin. The scale-like postcleithrum bears a few shallow grooves posteriorly.

Fins. All fins bear fringing fulcra. The incompletely preserved dorsal and anal fins are situated opposite each other within the rear half of the body. The lepidotrichia are articulated frequently throughout their length. The anal fin is slightly longer based than the dorsal. The caudal fin is preserved as isolated patches of lepidotrichia and fringing fulcra; all three resemble those of *Mesopoma carricki*. The pectoral fin consists of nine or more

fin rays which are articulated distally, and bifurcate at least once before reaching the trailing edge. The pelvic fin has a broader insertion than that of *M. carricki*. It consists of ten or more fin rays which are articulated throughout their length and bifurcate once, distally.

Squamation. The large, rhomboidal scales have a clearly defined anterodorsal process (Text-fig. 4B) and a serrated posterior edge. Two or more parallel grooves flank the anterior and ventral edges. Occasionally, faint diagonal, posteroventrally oriented ridges may be observed in the centre of the external surface, which originate from the serrated posterior edge. Scales adjacent to the post-temporals bear the most prominent ornament, lack an anterodorsal process, and acquire a convex posterior edge. The squamation is arranged in approximately thirty two, almost vertically oriented rows. Each has eight or more scales above and eight or more below the lateral line. The median fins are preceded by basal fulcra, and a series of caudal lies along the dorsal mid-line of the tail.

Mesopoma pancheni sp. nov.

Text-figs 6-7

Derivation of name. Named after Dr Alec L. Panchen, who supervised the original research on this material.

Holotype. NMS 1983.33.7.

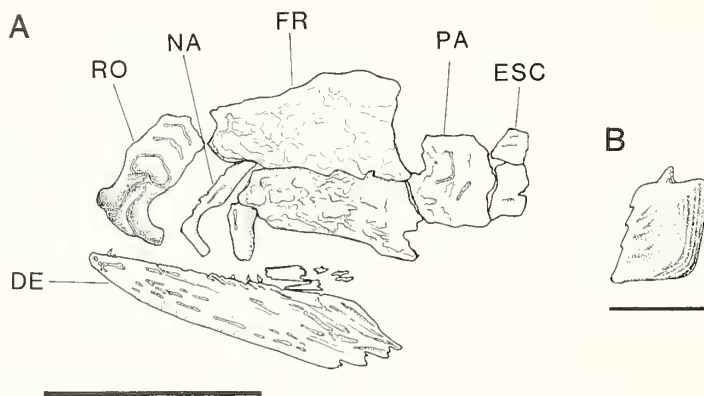
Referred specimens. The above-mentioned holotype, together with GLAHM V8283a-b; SPW 1941.

Horizon and locality. Shrimp member, Manse Burn Formation, Pendleian (Namurian) E₁ Zone, Lower Carboniferous. Bearsden, Glasgow, Scotland.

Diagnosis. Frontals forming W-shaped suture with rostronasal complex; rostral ornamented with three broad, posteriorly directed chevrons on posterodorsal surface; two or more basal fulcra preceding dorsal fin; three basal fulcra preceding anal fin; squamation arranged into thirty-five or more rows; scales have convex denticulated posterior edge in region behind post-temporals; dermal ornament consisting of distinct posteriorly directed chevrons, most prominent on scales surrounding dorsal mid-line, and four or more grooves parallel to anterior edge.

Discussion. *M. pancheni* may be distinguished from *M. carricki* on the basis of the following characters: a W-shaped rostronasal; frontal suture; incised posteriorly directed chevrons on rostral; denticulated scales bordering post-temporals; chevron-ornament on scales. None of these characters can be demonstrated to be ontogenetically precursive to the morphology of *M. carricki*.

Description. This is the rarest and least well known of three species of *Mesopoma* from Bearsden. *M. pancheni* appears to have been a slender, fusiform, species, not much more than 55 mm long. The length of the head, measured from the rostral apex to the rear of the operculogular series, is about 10 mm (Text-fig. 7).

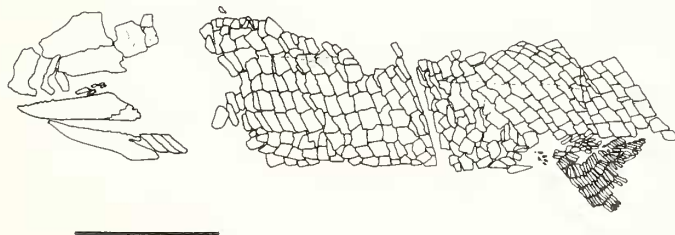


TEXT-FIG. 6. *Mesopoma pancheni* sp. nov. A, incomplete dermal skull of holotype, NMS 1983.33.7. Scale bar = 5 mm. B, anterior flank scale. Scale bar = 1 mm. Abbreviations: see Text-figure 2.

Skull and lower jaw. The maxilla, represented solely by a single median portion situated on specimen GLAHM V8283a, displays a few posteriorly directed ornamental grooves (these grooves are more vertically oriented than those of *M. carricki*). The marginal teeth are small and conical. The triradiate dermosphenotic passes the infraorbital canal from the dermopterotic to the dorsal apex of the posterior infraorbital. The dermosphenotic resembles closely that of *M. carricki*. The crescentic posterior infraorbital has an embayed posterodorsal region, indicating that one or more suborbitals may have been present. The extrascapular region of the skull table is unclear (ESC, Text-fig. 6A). A subrectangular dermopterotic with a convex ventral edge occupies the temporal region. Each subrectangular parietal has a convex anterior edge which projects into the embayed posterior edge of the frontal. The anteriorly narrow frontals combine to form a W-shaped suture with the posterior edge of the rostral and nasals.

Fronto-parietal dermal ornament consists of flattened ridges and tubercles, similar to those of *M. carricki*. The prominent rostral resembles that of *M. carricki*. The dermal ornament consists of a symmetrical arrangement of large ganoine tubercles which cap the apex of the snout. The dorsal portion bears a series of three broad, posteriorly directed chevron-shaped ridges. The nasal is smooth, with a discontinuous groove adjacent to the anterior edge overlying the sensory canal. Only the external surface of the lower jaw is known. The dentary is ornamented with a series of long grooves which radiate from the posteroventral corner. The dentition consists of uniformly sized, small conical teeth. A slender angular passes around the rear of the dentary. The surangular is unknown. Isolated narrow, subtriangular branchiostegal rays have faint shallow grooves radiating from the point of submandibular insertion.

Pectoral girdle. The subelliptical post-temporal has a posterior edge with a series of widely spaced denticulations. The supracleithrum is slightly more rhomboidal than that of *M. carricki*, but is otherwise similar. The dermal ornament consists of four parallel grooves which run parallel to the anterior and ventral edges. The cleithrum has a robust bipartite vertical blade with a ridged dermal ornament.



TEXT-FIG. 7. *Mesopoma paucheni* sp. nov., squamation of holotype, NMS 1983.33.7. Scale bar = 10 mm.

Fins. All fins bear fringing fulcra. The dorsal and anal fins are situated opposite each other in the rear half of the body. The dorsal fin is incompletely known, but appears to be similar to that of *M. carricki*. The lepidotrichia are articulated at frequent, even intervals throughout their length. The anal fin consists of about twenty five lepidotrichia; it is acuminate with an embayed trailing edge. The lepidotrichia resemble those of the dorsal fin. The pattern of bifurcation is unknown. The caudal fin is known only from isolated patches of lepidotrichia. The pectoral fin consists of an undetermined number of proximally unarticulated lepidotrichia. The posterior lepidotrichia display greater distal articulation. The pelvic fins are known only from isolated, incomplete lepidotrichia.

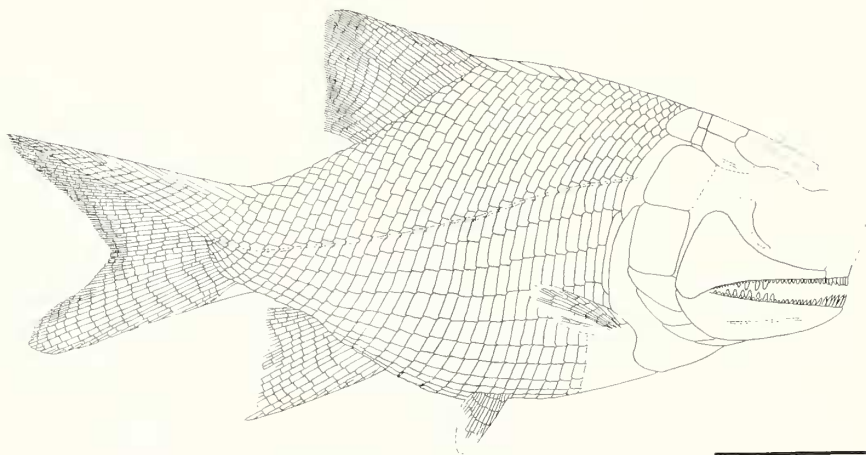
Squamation. The scales are large and rhomboidal, with a prominent anterodorsal angle (Text-fig. 6B). They are arranged into at least thirty-five vertically oriented rows. Next to the dorsal mid-line they develop a convex posterior edge. The dermal ornament is specifically characteristic: four or five sharply defined parallel grooves lie adjacent to the anterior edge, turning to follow the dorsal and ventral edges and occasionally bifurcating before fading posteriorly. The remainder of the surface is smooth if located on or near to the lateral line, but otherwise bears a series of posteriorly directed chevrons. The scales near to the post-temporals have a denticulated posterior edge. Only the proximal portion of the caudal lobe is known. The dorsal mid-line bears a series of caudal fulcra. The area preceding the origin of the hypochordal lobe shows fragments of a number of basal fulcra. A series of two or more basal fulcra precedes the insertion of the dorsal fin, and three basal fulcra precede the anal fin.

Infraclass ACTINOPTERI
Genus FREDERICHTHYS gen. nov.

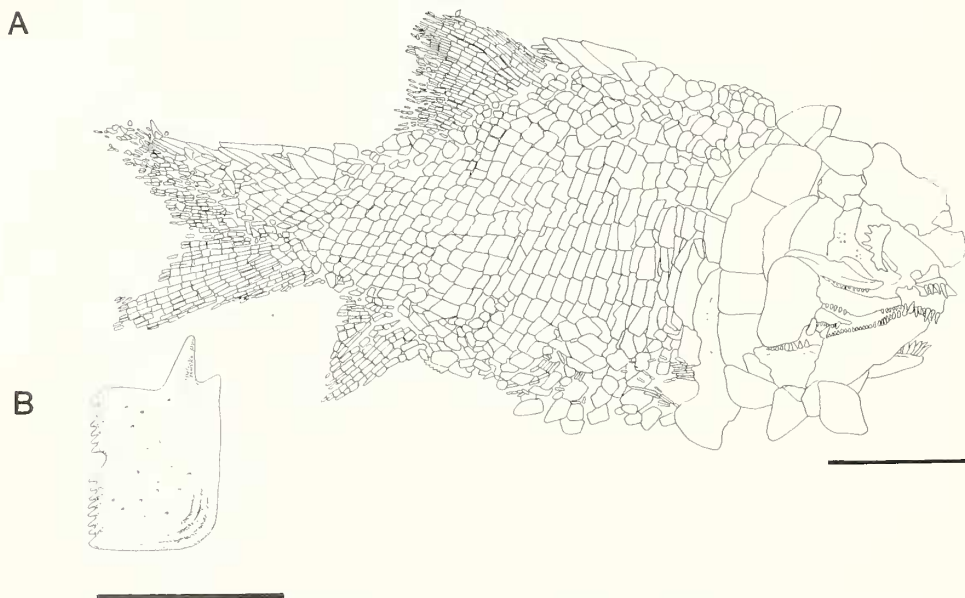
Type species. Frederichthys musadentatus sp. nov.

Derivation of name. After the nickname 'Fred fish' (+ 'ichthys', Greek, a fish) applied to the single known specimen of this genus whilst it was undergoing preparation and reconstruction.

Diagnosis. As that of the species.



TEXT-FIG. 8. *Frederichthys musadentatus* gen. et sp. nov., restoration. Scale bar = 10 mm.



TEXT-FIG. 9. *Frederichthys musadentatus* gen. et sp. nov. A, composite line drawing of holotype, GLAHM V8286a-b. Scale bar = 10 mm. B, anterior flank lateral line scale. Scale bar = 2 mm.

Frederichthys musadentatus, sp. nov.

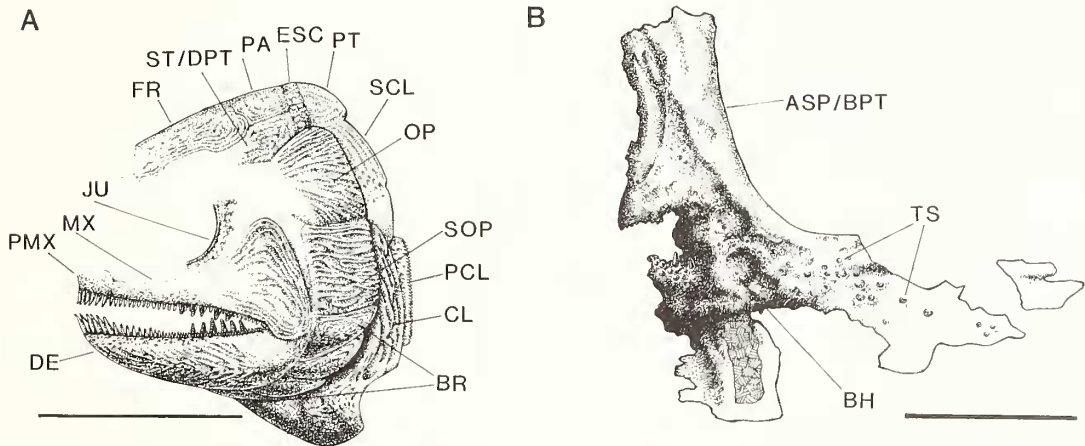
Plate 1, fig. 3; Text-figs 8–10

Derivation of name. New Latin *musa*, derived from the Arabic *muze* meaning banana or plantain, and late Latin *dentatus* meaning toothed, alluding to the shape of the anteriormost teeth.

Holotype. GLAHM V8286a–b, the only known specimen.

Horizon and locality. Not identified *in situ*, but probably from the Shrimp member, Manse Burn Formation, Pendleian (Namurian) E₁ Zone, Lower Carboniferous, Bearsden, Glasgow, Scotland.

Diagnosis. Maxilla with rounded triangular posterior expansion; mandible deep posteriorly; moderately enlarged premaxillae; mandible and palate thickly ossified; large conical teeth present on palate and medial surface of lower jaw; marginal dentition consisting of small conical teeth increasing in size and externally oriented curvature towards anterior of gape; jaw suspension near-vertical; parasphenoid well ossified with robust lateral processes; frontals with rounded, expanded anterolateral and posterolateral corners; opercular almost equal in size to subopercular; branchiostegal series reduced to four large plates; postcleithrum present; dorsal fin insertion longer than anal



TEXT-FIG. 10. *Frederichthys musadentatus* gen. et sp. nov. A, restoration of skull and pectoral girdle, showing dermal ornament. Scale bar = 10 mm. B, GLAHM V8286b, incomplete parasphenoid (cross-hatch indicates adhering matrix). Scale bar = 2 mm. Abbreviations: see Text-figure 2.

fin insertion; no fringing fulcra; ganoine scales with anterodorsal process, arranged in almost thirty three near-vertical sigmoid rows; body gibbose with deep scales in flank region; six or more fulcral scales preceding dorsal fin; one fulcral scale preceding caudal fin; pair of denticulated anal scales preceding anal fin; basal fulcra on dorsal margin of tail.

Discussion. This unusual, gibbose (moderately deep-bodied) fish, like most Bearsden actinopterygians, has little preserved of its internal structure. The snout, circumorbital, cheek, and temporal regions of the dermal skull are also missing.

Description. The total length of *Frederichthys* is 57 mm. The length of the head accounts for 14 mm (measured from the anterior of the gape to the rear of the opercular series), and the maximum depth of the body is 23 mm. *Skull and lower jaw.* The dermal ornament of the skull, lower jaw, and pectoral girdle is illustrated in Text-figure 10A. The maxilla has a large, triangular postorbital region, indicating that the jaw suspension was near-

vertical. The marginal dentition increases in size anteriorly, mirroring the mandibular tooth distribution; the trend of increased tooth size passes forwards to the premaxillae. The insertion of the larger, tusk-like teeth is uncertain: they may have been born on the dermopalatines or a mesial ridge on the maxilla. An incompletely preserved posterior infraorbital has a ragged posterior edge, and appears to have been large and crescent-shaped. Four anteroposteriorly narrow, rectangular extrascapulars overlap the anterior margins of the post-temporals. Each of the subrectangular parietals has a notched anterolateral corner; neither appears to have a pit line. An incomplete, broad dermopterotic (DPT, Text-fig. 10A), carries the otic section of the infraorbital canal. The impression of a large otolith lies within the temporal region; the diameter appears to be about half the length of the restored dermopterotic. The frontals are about twice the length of the parietals; each has greatly expanded posterolateral and anterolateral corners. The anterolateral corner extends as an elongate process flanking an embayment for the derm-ethmoidal bones. Each incomplete premaxilla is rectangular, robust and ornamented with numerous small pits on the external surface; the dorsal edges are incomplete. Large curved teeth, identical to the anteriormost mandibular teeth, are borne on a mesial ridge adjacent to the ventral margin. A T-shaped parasphenoid (Text-fig. 10B) with an anteriorly expanded median ramus lies beneath the orbital region. The buccal surface bears numerous sockets for peg-like teeth. Mid-posteriorly, a circular depression may mark a closed buccohypophyseal foramen, flanked laterally by robust semicylindrical ascending or basiptyergoid processes (ASP/BPT, Text-fig. 10B). These bear a complex system of grooves posteriorly. The greatly thickened palatoquadrate is preserved in cross-section above the maxilla, bearing further peg-like teeth. The lower jaw is well ossified and moderately deep. The full extent of the individual ossifications cannot be determined. The dentition is arranged into at least two series, one marginal, and the other born on a robust dorsomedial ridge. The marginal dentition consists of sharp conical teeth which increase in size anteriorly, accompanied by reorientation of the crowns of the largest to face anterolaterally. The constricted bases of the anteriormost teeth resemble closely those of *Mesolepis* Young, which were described by Rankin (*in* Traquair 1879) as 'Minié bullet-shaped'. Tusk-like teeth borne on the dorsomedial surface of the mandible lie towards the rear of the jaw. The broad subrectangular opercular is incomplete anteriorly. The dotted line on the reconstruction indicates its probable full extent. The slightly taller and narrower subopercular has a denticulated posterior edge. There are only four large plates within the branchiostegal series. The most posterodorsal of these is triangular; the central pair are of sub-parallelogram form; the anterior plate is more acutely triangular and extends to a point approximately half-way along the ventral surface of the lower jaw.

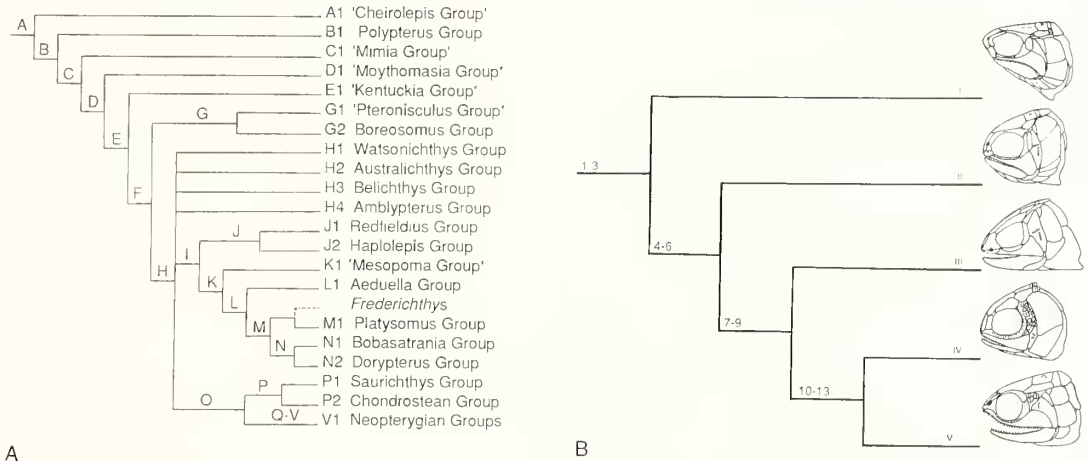
Pectoral girdle. The semi-elliptical post-temporal has a denticulated posterior border and a smooth anterior margin overlapped by the extrascapulars. The supacleithrum has a smooth posterior edge; the dorsal region contains the lateral line canal. The cleithrum has an exceptionally tall bipartite vertical blade, and a largely mesially curved ventral lamina. The postcleithrum is large, rectangular with a serrated posterior edge, and approximately double the size of the flank scales.

Fins. The leading edges of all fins consist of terminal lepidotrichia; no fringing fulcra have been found. The dorsal and anal fins are trapezoidal, broad-based, and situated in the rear half of the body (Text-fig. 8). The dorsal fin consists of thirty one or more lepidotrichia which articulate throughout their length and bifurcate at least once before the trailing edge. Neither of the fins appears to have been emarginated posteriorly. The anal fin is more acuminate than the dorsal fin; the insertion is shorter, and it is composed of fewer lepidotrichia (twenty or more). The principal lepidotrichia of the anal fin are broader and bifurcate less often than those of the dorsal. The caudal fin consists of forty or more frequently articulated lepidotrichia which bifurcate at least once distally, most commonly twice. The tail is equilobate with a moderately emarginating posterior edge. The pectoral fins appear to be small, consisting of only nine or more lepidotrichia which articulate up to four or five times, and bifurcate once, distally. The pelvic fins are situated half-way between the pectoral girdle and the anal fin. Each is moderately broad-based, consisting of ten or more frequently articulated lepidotrichia.

Squamation. The rhomboidal scales have a well-developed anterodorsal angle, of the type found in fusiform species. Dermal ornament consists of shallow grooves which originate from the denticulated posterior edge; three or more parallel grooves lie next to the anteroventral corner. The trunk bears about thirty three near-vertical scale rows. The number of scales per row increases in the central flank region and below the insertion of the dorsal fin. The caudal prolongation is moderately up-turned. Scales with a convex posterior edge and prominent dermal ornament lie adjacent to the rear of the skull table. Basal fulcra lie on the dorsal mid-line of the tail, and the hypochordal lobe is preceded by a single, elongate ventral caudal scale. The dorsal fin is preceded by a series of six or more fulcra. A pair of elongated, rhomboidal anal scales precede the insertion of the anal fin. These have a denticulated posterior edge, and lie across the fourteenth and fifteenth scale rows.

DISCUSSION

Members of *Mesopoma* are generally described as palaeoniscids, although it is now widely agreed that these constitute a paraphyletic group of mostly Palaeozoic actinopterygians (Cladistia + Actinopteri). The revised classification was established principally by Patterson (1982) and Gardiner (1984), and elaborated upon by Lauder and Liem (1983), Long (1988), and Gardiner and Schaeffer (1989). Gardiner (1984), in particular, demonstrated that the majority of the palaeoniscids should be treated as 'plesion' (Patterson and Rosen 1977) members of the neopterygian stem-group, and that *Mesopoma* lay within this assemblage. However, Gardiner and Schaeffer (1989) have reassessed this pattern of relationships (their cladogram is depicted in Text-fig. 11A). In contrast to Gardiner (1984), the extant Chondrostei were found to share more characters with the Neopterygii (*sensu* Patterson 1982) than with most palaeoniscids. Consequently, genera such as



TEXT-FIG. 11. A, cladogram of major groups of early actinopterygians showing taxonomic positions of species considered in this paper (cladogram adapted from Gardiner and Schaeffer 1989, fig. 12; for definitions of all terminal groups and complete character list see this reference). Selected characters of lettered nodes discussed in text; taxa within quotation marks may be paraphyletic. B, alternative cladogram of selected taxa rooted at node I in Gardiner and Schaeffer's cladogram. Characters 1–13 discussed in text. Taxa illustrated: i, *Mesopoma carricki* (exemplifying the genus *Mesopoma*); ii, *Canobius ramisayi*, after Moy-Thomas and Bradley Dyne 1938 (exemplifying the genus *Canobius*); iii, *Protohaplolepis scoticus*, after Lowney 1983 (exemplifying the family Haplolepidae); iv, *Aeduella blainvillei* after Heyler 1969 (exemplifying the family Aeduellidae); v, *Phlyctaenichthys pectinatus* after Hutchinson 1973 (exemplifying the infraorder Redfieldiformes).

Mesopoma are now considered to be 'lower', taxonomically, and, together with other taxa, form an unresolved polytomy within the stem-group of the Actinopteri (Chondrostei + Neopterygii).

In agreement with Gardiner and Schaeffer (1989), *Mesopoma* shares the following characters (as listed in the generic diagnosis) with the Actinopterygii: ganoine scales; scales with anterodorsal process; dentary includes mandibular sensory canal; dermohyal; basal fulcra on dorsal margin of tail; peg and socket scale articulation; postcleithrum.

This paper is not intended to be an exhaustive examination of Gardiner and Schaeffer's cladistic analysis. Therefore not all of their character list will be discussed. However, this revision has identified certain unsatisfactory choices or positions of characters. The following basal actinopterygian characters are taken from Node A, table 1 and figure 12, of Gardiner and Schaeffer's paper (Text-fig. 11A):

1. Otoliths in part composed of vaterite.
6. Dermosphenotic T-shaped, in contact with nasal bone.
18. Tail with hinge line (caudal inversion).

The first autapomorphy (1) of Gardiner and Schaeffer's list, that actinopterygian otoliths are *in part* (my italics) composed of vaterite, is a subtle restatement of character 10 of Gardiner's (1984) earlier list: otoliths formed of vaterite. This statement derives from Carlstrom (1963) via Lovtrup (1977) and Patterson (1982).

Almost all gnathostome otoliths consist of calcium carbonate, which occurs in three crystalline forms: calcite, aragonite, and vaterite (the least stable); the vast majority consist of aragonite (Carlstrom 1963). Otoliths occur as statoliths (large 'ear stones') or statoconia (minute 'ear dust'). The otic labyrinth of *Polypterus* contains both aragonite statoliths and vaterite statoconia. *Acipenser guldenstadti* and *A. sturio*, the Russian and Atlantic sturgeons, have vaterite statoliths and statoconia. *Lepisosteus* and *Amia* have aragonite statoliths and vaterite statoconia, and Carlstrom considered teleost otoliths to consist solely of aragonite statoliths. The distribution of vaterite within the Actinopterygii appeared to be restricted to the statoconia of non-teleosts, and the statoliths of certain chondrosteans. However, Gauldie *et al.* (1986b) recorded the presence of statoconia in four neoteleostean taxa. Furthermore, Gauldie (1986) described experimentally induced vateritic statoliths in the chinook salmon (*Onchorhynchus tshawytscha*) and noted occurrences in other taxa (e.g. the dab, *Limanda limanda*), including the replacement of calcite by vaterite in certain diseases of the human ear. The erratic distribution of vateritic otoliths indicates that Gardiner and Schaeffer's character (1) is insufficiently precise. Maisey (1987) suggested an alternative characterization of the Actinopterygii: the presence of 'smaller statoconia of vaterite (absent in teleosts); separate lagenar and saccular otoliths', the first part of which appears tenable.

The second part of Maisey's characterization of the Actinopterygii (separate lagenar and saccular otoliths) is inconsistent with the presence of only a single, large statolith in each otic capsule of *Mesopoma? smithsoni*. Single otoliths are found in several other Bearsden actinopterygians (Coates 1988), *Mimia toombsi* (Gardiner 1984), and *Rhadiniichthys canobiensis* (Moy-Thomas and Bradley Dyne 1938, pl. I fig. A, showing natural cast of statolith), whereas extant actinopterygian otic capsules each contain three statoliths. Talimaa (*in* Nolf 1985) interpreted the oldest known otoliths, from the Lower and Middle Devonian, as actinopterygian because they, too, consist of three distinct types: saccular, lagenar, and utricular, resembling the sagitta, asteriscus, and lapillus of teleosts. Schultze (1988, 1990) accepted Talimaa's interpretation, although these otoliths are phosphatic and isolated from skeletal remains. Phosphatic otoliths are extremely rare within the gnathostomes (Maisey 1987 cited apatite statoconia as an autapomorphy of cyclostomes). Although diagenetic processes may alter fossil otolithic composition (Tucker 1990), 'metasomatic mineralisation' (Maisey 1988) from calcite to apatite is extraordinarily unlikely (Schultze 1990). Furthermore, although both Devonian and teleost statoliths have central sulci, statoliths preserved within early actinopterygians have a rim-located sulcus, resembling closely the lapillus and (single) saccular statolith of the dipnoan *Neoceratodus forsteri* (Gauldie *et al.* 1986a). The sacculus of *Latimeria* (Millot and Anthony 1965) similarly contains only a single statolith with an apparently rim-located sulcus. These single saccular statoliths should not necessarily be homologized with the sagitta. Extant non-teleostean actinopterygian sacculae contain both the sagitta and asteriscus, of which the asteriscus is usually the larger (Nolf 1985 misinterpreted the small cladistian sagitta for the lapillus (Coates 1988)).

In conclusion, Talimaa's interpretation of the Devonian otoliths is rejected. They are unlike actinopterygian statoliths in chemical composition; they differ morphologically from stem-group actinopterygian statoliths; they are not associated with actinopterygian skeletal remains. Out-group comparison suggests that the actinopterygian plesiomorphic condition is to have a single saccular calcitic statolith with a rim-located sulcus. This suggests that paired statoliths (sagitta + asteriscus) within the sacculus have been derived independently within the Cladistia and the Actinopteri. Because of this, Maisey's supplementary actinopterygian apomorphy (separate lagenar and saccular otoliths) is rejected. Maisey also failed to distinguish between the otic recesses and their contents, and to recognize that in extant actinopterygians, a distinct lagena is present only within the Teleostei. Schultze's (1990) hypothesis that three pairs of otoliths are a basic feature of teleostomes

(uniting acanthodians with osteichthyans) is also rejected. Available data suggests that the basic osteichthyan saccular recess contains a single statolith.

The hypothesis that dermosphenotic:naasal contact (6) is primitive for actinopterygians is accepted, but not the linkage of this pattern to the 'T' or tau form of the bone. This refinement of an otherwise plesiomorphic character loses potential taxonomic value if applied loosely to a variety of sub-triangular forms of dermosphenotic, as found in most stem-group actinopterygians (see Gardiner and Schaeffer 1989, fig. 2). In contrast, the dermosphenotic of *Mesopoma*, where known, has three distinct rami (Text-fig. 2A). This form of dermosphenotic is considered to be more precisely T-shaped; it aids the characterization of the genus.

A caudal scale row inversion is accepted as plesiomorphic for actinopterygians (18), but not the concomitant appearance of a distinct hinge-line between trunk and tail squamation. *Cheirolepis* (Pearson and Westoll 1979), *Howqualepis* and other early actinopterygians described by Long (1988), and many of the Bearsden (Coates 1988) and Bear Gulch (Lowney 1980) taxa, including *Mesopoma*, show no distinct hinge-line.

At node B, *Mesopoma* shares the presence of a postcleithrum.

At node C, *Mesopoma* shares the presence of fringing fulcra on all fins.

At node D, *Mesopoma* shares the presence of supra-angular on the mandible.

At node E, *Mesopoma* shares the presence of suborbital bones.

At node F, *Mesopoma* shares the presence of a ceratohyal bar composed of two cartilages or ossifications (Lowney 1980; Text-fig. 11A).

At node G, *Mesopoma* shares the presence of a robust opercular process on the hyomandibula (Lowney 1980).

The presence of an opercular process was not anticipated by Gardiner and Schaeffer: node G defines the small monophyletic radiation of pteronisculids and boreosomids, fishes which share no other clear synapomorphies with *Mesopoma*. Opercular processes are probably more widely distributed amongst early actinopterygians than is suggested by Gardiner and Schaeffer. For a more detailed discussion of the hyoid arch in early actinopterygians, see Kazantseva 1974; Patterson 1982 and Veran 1988.

At node H, *Mesopoma* shares the presence of a dermopterotic.

At node I, *Mesopoma* shares a reduction in the number of branchiostegal rays below the primitive 12 or 13 (except '*M. becketense*' (attrib. Lowney, Text-fig. 12i)), and a dermopterotic which never normally overlaps more than one third of the dermosphenotic.

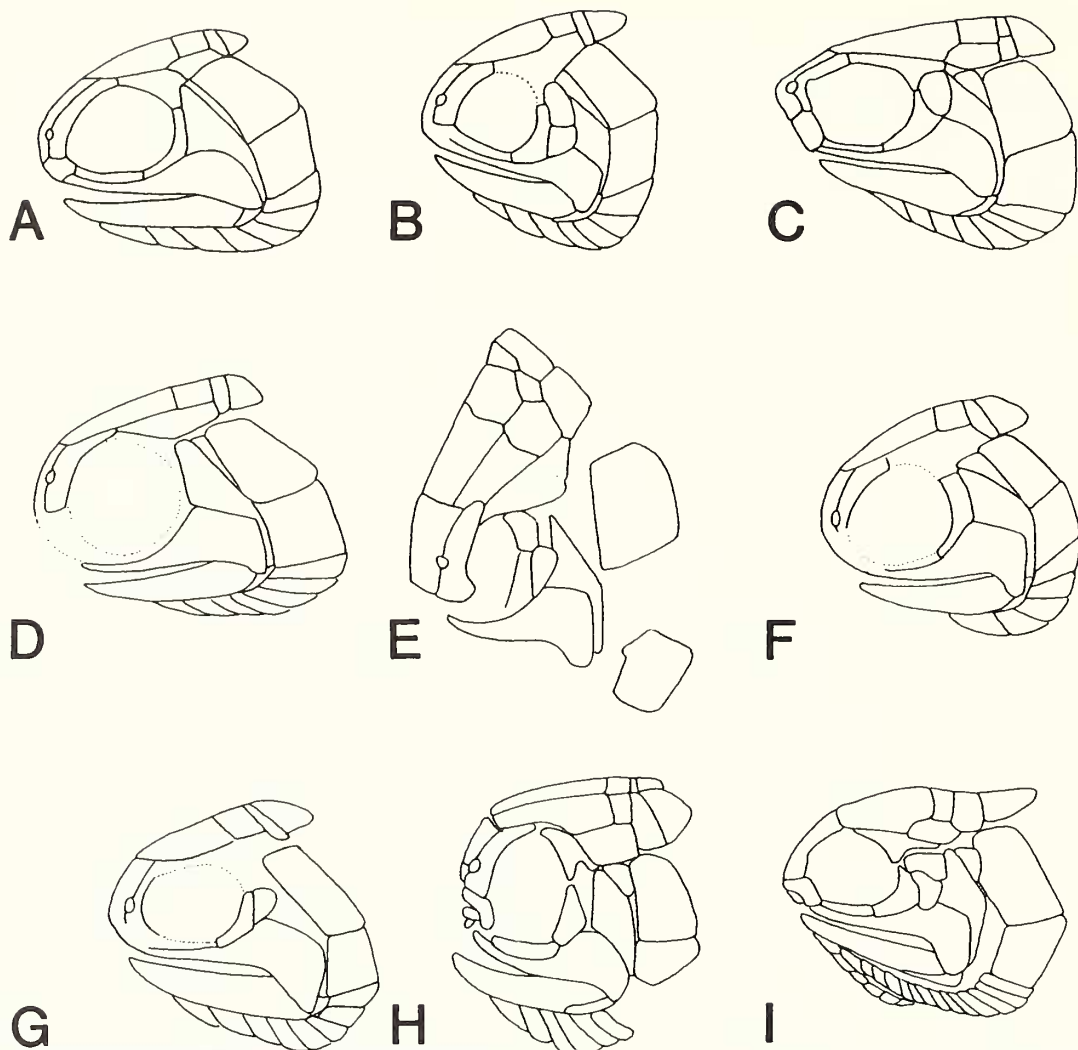
Gardiner and Schaeffer's cladistic analysis therefore places *Mesopoma* within the polychotomous radiation of stem-group actinopteranans.

At node J, no characters are shared.

The absence of shared characters at node J corroborates Lowney's (1983), and Gardiner and Schaeffer's (1989) independent refutations of Westoll's (1944) influential evolutionary sequence (e.g. Moy-Thomas and Miles 1971), which led from *Mesopoma*, via *Canobins* to a hypothetical ancestor of the haplolepidids. However, this transformational series recurs within an alternative phylogeny (Text-fig. 11B) discussed below.

At node K, *Mesopoma* should display three characters which unite it with its own and four further groups of Carboniferous to Permian actinopteran genera: the presence of a more vertical suspensorium; a reduced preopercular; the absence of suborbital bones in the cheek region.

Gardiner and Schaeffer's *Mesopoma*-group includes *Mesopoma*, *Canobins* Traquair, 1881 *sensu* Moy-Thomas and Bradley Dyne 1938, and *Styracopterns* Traquair, 1895 *sensu* Gardiner 1985. The description of the type species, *Mesopoma pulchellum*, is central to the diagnosis of the entire group and its interrelationships within the actinopteran stem-group radiation. Gardiner and Schaeffer's restoration of the dermal skull of *M. pulchellum* is reproduced as Text-figure 12A. However, the proportions and complement of dermal skull bones differ from those of Moy-Thomas and Bradley Dyne's (1938) reconstruction (Text-fig. 12B). Most obviously, the suborbital bones depicted by Moy-Thomas and Bradley Dyne have been removed. The figure legend of Gardiner and Schaeffer's illustration (1989, p. 174, fig. 18) states that their new reconstruction of *M. pulchellum* is based



TEXT-FIG. 12. *Mesopoma* species, skulls in lateral view. A, *M. pulchellum* (after Gardiner and Schaeffer 1989). B, *M. pulchellum* (after Moy-Thomas and Bradley Dyne 1938). C, *M. carricki* sp. nov. D, *M. macrocephalum* (after Moy-Thomas 1938). E, *M. ardrossense* (after Moy-Thomas 1938). F, *M. politum* (after Moy-Thomas and Bradley Dyne 1938). G, *M. crassum* (after Moy-Thomas and Bradley Dyne 1938). H, *M. macrocephalum* (after Lowney 1980). I, *M. becketense* (after Lowney 1980).

upon Moy-Thomas and Bradley Dyne's (1938) illustration, and specimen BM(NH) P14310. Significantly, no reference is made to the type specimen (m611d in the Geological Survey, Murchison House, Edinburgh).

The new reconstruction of *M. pulchellum* resembles closely *M. macrocephalum* as restored by Moy-Thomas (1938) (Text-fig. 12D), rather than Lowney (1980) (Text-fig. 12H). Both reconstructions of *M. macrocephalum* showed that it lacked suborbitals, a character which it formerly shared uniquely with *M. politum* (Text-fig. 12F) within this genus. Therefore, out of seven species of *Mesopoma* in which the cheek region is known, four must now be excluded, because they possess suborbitals. The misidentification of specimen BM(NH) P14310 (the source of Gardiner and Schaeffer's redescription of *M. pulchellum*) is probably the cause of this unexpected taxonomic

revision. In fact, this specimen is catalogued and labelled clearly as *M. macrocephalum*. The specimen is in good condition, and is sufficiently similar to the type, NMS 1901-227-2, to leave this diagnosis in no doubt.

If the new reconstruction of *M. pulchellum* is based upon a misidentified specimen, then the specific diagnosis can revert to Moy-Thomas and Bradley Dyne's (1938), and the generic diagnosis may be revised to the form proposed earlier in this paper. The presence or absence of suborbital bones can be rejected as a diagnostic character at the generic level. Jain (1985) demonstrated surprisingly variable dermal bone patterns in the cheek region of the extant halecomorph *Annia calva*. In this single species the number of canal-bearing infraorbito-suborbitals varies from one to three or more between and even within (bilaterally asymmetric) individuals. This suggests that the arrangement of anamestic suborbitals in a fossil genus which displays a variety of cheek patterns may be unreliable as a taxonomic indicator.

The removal of the 'suborbital' synapomorphy from node K of Gardiner and Schaeffer's cladogram (Text-fig. 11A) does not affect their characterization of the *Mesopoma* group. Autapomorphies of mesopomids at node KI are listed as:

- i, a near-vertical suspensorium;
- ii, a reduced preoperculum;
- iii, a postorbitally reduced maxilla;
- iv, a subopercular subequal to or larger than the opercular;
- v, a T-shaped dermosphenotic.

Characters i-iii of this list are discussed below, because they are effectively identical to the remaining synapomorphies at node K. Character iv is probably valueless, and character v is recycled from node A (see above). The *Mesopoma* group therefore appears to be paraphyletic, and if retained in Gardiner and Schaeffer's scheme, should be placed within quotation marks (cf. 'Cheirolepis Group', Text-fig. 11A).

If the 'absence of suborbitals' character is removed, then the aeduellids, platysomoids, bobasatraniids, and dorypterids (Text-fig. 11A) are united solely on the basis of having a 'more or less' (Gardiner and Schaeffer 1989) vertical suspensorium, and a reduced, sickle-shaped preopercular. These two closely linked synapomorphies provide little basis for the construction of a major phylogenetic hypothesis incorporating seventeen morphologically diverse genera. An alternative hypothesis of the interrelationships of the *Mesopoma*, *Aedulla*, *Haplolepis*, and *Redfieldius* group constituents (Text-fig. 11B), also rooted at node I of Gardiner and Schaeffer's cladogram, may be constructed using the following characters:

- 1, reduced branchiostegal series;
- 2, dermopterotic normally never overlaps more than one-third of dermosphenotic;
- 3, jaw articulation sited anteriorly relative to the parieto-extrascapular suture;
- 4, vertical jaw suspension;
- 5, reduced rostral projection (= terminal gape);
- 6, triangular preopercular bearing one or more pit-lines;
- 7, two or fewer branchiostegals;
- 8, uninterrupted naso-rostral suture (= loss of anterior nares: Schaeffer 1984);
- 9, dentition reduced or absent from premaxillae;
- 10, premaxillae excluded from gape;
- 11, supraorbital canal enters dermopterotic;
- 12, numerous suborbitals at head of preopercular;
- 13, ramose infraorbital canal.

The data upon which these characters are based were obtained from recent descriptions and reviews which provided alternatives to Gardiner and Schaeffer's reinterpretations of many of the selected taxa. In Moy-Thomas and Bradley Dyne (1938), *Canobius ramsayi* (Text-fig. 11Bii) possesses preopercular pit-lines and suborbitals. The sensory canal system penetrates the base of the median derm-ethmoidal shield, which corroborates the interpretation of this bone (and that of *Mesopoma*, see description) as a rostral rather than post-rostral. A vertical suspensorium and the lack of a

rostrum unite *Canobius* with numerous other genera, illustrating the paraphyletic nature of the *Mesopoma* group. Haplolepidids are exemplified by the earliest and least-derived genus known, *Protohaplolepis* (Lowney 1983) (Text-fig. 11Biii). Heyler's (1969) description of *Aeduellia* (Text-fig. 11Biv), exemplifying the Aeduellidae, lacks an anterior nostril, the supraorbital canal enters the dermopterotic rather than the dermosphenotic, numerous suborbitals lie above a short triangular, pit-lined, preopercular, and the infraorbital canal bears an unusually profuse array of sub-branches. Many of these characters are shared with *Phlyctaenichthys* (Hutchinson 1973) (Text-fig. 11Bv), an early brookvaliid, exemplifying the Redfieldiformes (*sensu* Schaeffer 1984). Although unknown in this genus, other brookvaliids have a pit-lined preopercular. The haplolepid: aeduellid: redfieldiform relationship is more robust than the haplolepid: redfieldiform sister-grouping proposed by Gardiner and Schaeffer (node J, Text-fig. 11A, characterized by the presence of a single ventral nostril, a single branchiostegal ray, and an enlarged postcleithrum).

In the alternative cladogram (Text-fig. 11B), *Mesopoma* and *Canobius* are plesion taxa, contributing to the stem-group of three major early actinopteran radiations: the haplolepidids, aeduellids, and redfieldiforms. This arrangement provides an alternative to Blot's (1966) and Heyler's (1969) unsatisfactory proposals of *Paramblypterus* as a sister group to the redfieldiforms (a problem most comprehensively discussed in Schaeffer 1984). Morphological trends include increased suspensorial angle, fragmentation of the dermal cheek-cover, exclusion of the premaxillae from the gape, and reduction of the gular-branchiostegal apparatus. The sequence of cladogenic events is consistent with the earliest known occurrences of each taxon: *Mesopoma* and *Canobius* from the Viséan (Moy-Thomas and Bradley Dyne 1938); *Protohaplolepis* from the Namurian (Lowney 1983); aeduellids, cf. *Bourbonella*, from the Upper Pennsylvanian (Gottfried 1987); redfieldiids from the Upper Permian (Hutchinson 1973).

A detailed discussion of the incorporation of deep-bodied early actinopterans into the revised cladogram is beyond the scope of this paper. However, characters 1–6 are present in the amphicentrids, and characters 9–10 suggest a separate origin for *Platysomus* and closely related taxa. This is consistent with subsequent discussion of the potentially diphyletic origin of the Platysomoidei (see below).

The geographical and stratigraphical distribution of the genus *Mesopoma* is relatively restricted. *M. pulchellum*, *M. politum*, and *M. crassum* are all known from the Viséan Calciferous Sandstone Measures of Glencartholm, Dumfriesshire. *M. macrocephalum* originates from the Pumpherstone Oil Shales of West Lothian, and *M. ardrossense* from the *Crangopsis* bed at Ardross, Fifeshire. Both the latter localities also lie within the Viséan Calciferous Sandstone Measures. The remaining four species all date from the Basal Namurian. *M. carricki*, *M. ? smithsoni*, and *M. pancheni* are known from Bearsden, Glasgow, whilst '*M. becketense*' (the only non-Scottish species) is known from Bear Gulch, Montana, USA.

In contrast to the new species of *Mesopoma*, *Frederichthys* bears only a limited resemblance to any other group of early actinopterans, including those that are either gibbose or rhombic-bodied. Its taxonomic position can be established only in so far as it shares the following synapomorphies with node A of Gardiner and Schaeffer's (1989) cladogram (Text-fig. 11A): two pairs of extrascapulars; dentary with enclosed sensory canal; single dorsal fin; basal fulcra bordering upper lobe of caudal fin.

At node B, *Frederichthys* shares the presence of a postcleithrum.

At node C, *Frederichthys* lacks the presence of fringing fulcra on the leading rays of all fins: the only anatomical feature which can be compared usefully with Gardiner and Schaeffer's scheme.

Frederichthys displays no clear synapomorphies with nodes D to G.

At node H, *Frederichthys* is considered to share the presence of a dermopterotic. This provides the most parsimonious interpretation of the incomplete temporal bone in the skull table (ST/DPT, Text-fig. 10A) with regard to subsequent synapomorphies.

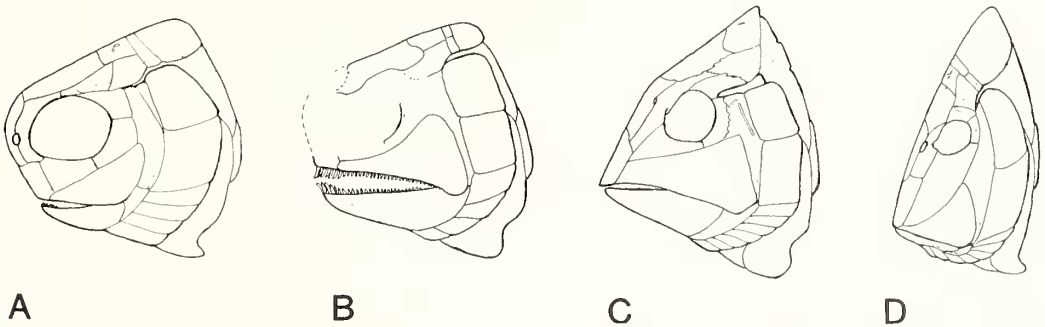
At node I, *Frederichthys* shares a reduced number of branchiostegal rays.

At node K, *Frederichthys* shares a 'more or less' vertical suspensorium.

At node L, *Frederichthys* probably shares a blunt and rounded snout. This character is implied solely by the distribution of fossil material.

At node M, *Frederichthys* shares (vaguely) peg-like teeth; a thickened palate rather than crushing toothplates; a deep, laterally compressed body.

Node M lies at the base of the radiation of deep-bodied early actinopterygians, which have been subdivided by Gardiner and Schaeffer into three groups: platysomids, bobasatranids, and dorypterids. This effectively reconstitutes the sub-order Platysomoidei (Romer 1966; Moy-Thomas and Miles 1971; Carroll 1988). The platysomoids have a long historical tradition which dates back to Young's (1866) *Lepidopleuridae*. Similarly, the monophyly of this group has been in doubt for over half a century, because the characters used to assign actinopterygians to the Platysomoidei are essentially modifications caused by differential growth; therefore common to all actinopterygians with



TEXT-FIG. 13. Platysomid skulls in lateral view. A, *Paramesolepis tuberculata* (after Moy-Thomas and Bradley Dyne 1938). B, *Frederichthys musadentatus* gen. et sp. nov. C, *Amphicentrum crassum* (after Coates 1988). D, *Platysomus superbus* (after Moy-Thomas and Bradley Dyne 1938).

a deep body (Moy-Thomas 1939). Gardiner and Schaeffer's platysomid group contains members of the two families formerly included in the Platysomoidei: the Platysomidae and the Amphicentridae. The amphicentrids (synonymous with the chirodontids) consist of forms with a crushing dentition of broad toothplates, and the platysomids of forms with more conventional teeth. The most extremely modified, and most completely described members of each family are the genera *Amphicentrum* Young, 1866 (Traquair 1875; = *Cheirodnis* Traquair, 1879; Bradley Dyne 1939; Coates 1988) (Text-fig. 13c) and *Platysomus* Agassiz, 1833 (Traquair 1879; Moy-Thomas and Bradley Dyne 1938; Campbell and Phuoc 1983) (Text-fig. 13d). Gardiner and Schaeffer diagnosed their *Platysomus* group on the basis of the maxilla approaching a rounded, right-angled triangle; the premaxillo-antorbital enlarged and elongated dorsally; the mandible deep posteriorly, tapering anteriorly. *Frederichthys*, despite the incompleteness of the material, exhibits the first and third of these criteria, and the dorsal extent of the premaxilla is unknown.

Clustered around *Amphicentrum* and *Platysomus* are a number of less specialized and more poorly known forms. From amongst these, the most likely candidate for a sister-group relationship with *Frederichthys* is *Paramesolepis* Moy-Thomas and Bradley Dyne 1938 (Text-fig. 13A). *Paramesolepis* is the least-derived member of the *Platysomus* group. Like *Frederichthys*, its most striking features (the pattern of the dermal skull, the elongated dorsal and anal fins) are products of differential growth associated with its gibbose shape. They are insufficient to commit it to a closer relationship with either of the amphicentrids or platysomids.

Frederichthys and *Paramesolepis* both have a branchiostegal series which consists of four broad plates located at the rear of the mandible. The marginal dentition of *Paramesolepis* is restricted to the anterior end of the jaws, and consists of a short series of small sharp pointed teeth. The marginal dentition of *Frederichthys* is reduced posteriorly, and anteriorly consists of outwardly oriented, curved, sharp pointed teeth. Differentiation along the tooth row is extremely unusual in early

actinopteran. It is therefore suggested that these two genera display different expressions of the same character. Although it was noted in the systematic description that the teeth of *Frederichthys* individually resemble those of *Mesolepis*, there is no further evidence to indicate a close relationship between these genera. *Mesolepis* (Traquair, 1907) appears to resemble *Amphicentrum* or *Eurynotus* more closely than *Frederichthys*.

The platysomid, bobasatraniiid, and dorypterid groups (Text-fig. 11A) require a major revision. Gardiner and Schaeffer's analysis neglected Campbell and Phuoc's (1983) paper on *Ebenaqua* and *Platysomus gibbosus*, which suggests a close relationship between *Platysomus* and *Bobasatrania* White, 1932. Furthermore, the Bearsden site has yielded a considerable quantity of new anatomical data concerning *Amphicentrum* (Text-fig. 13C, after Coates 1988), which is currently being prepared for publication.

Finally, the unusual morphology of *Frederichthys* requires a short note on its probable function in life. The gross functional morphology of extant actinopterygians of various body forms has been described by Keast and Webb (1966). In summary, their comments on the swimming of gibbose fish are as follows: the large lateral area prevents rolling and thereby provides considerable stability; pitch is controlled by the pectoral and pelvic fins, and asymmetrical vertical forces generated by these fins can tilt the body to any required angle; enlarged dorsal and anal fins are necessary to control yaw when swimming forwards, which is often assisted by rowing movements by the pectoral fins.

The unusual dentition and reinforced palate indicate that *Frederichthys* was a specialized feeder. It is difficult to propose an extant analogue because of the radical changes that have occurred to the actinopterygian feeding mechanism. However, it is possible that it was similar in habit to the sheephead wrasse *Pimelometopon*. These gibbose fish also have robust jaws and anterior teeth which point forwards and outwards (although these are chisel-shaped). The sheepheads feed in kelp beds in rocky areas, and prey on slow-moving benthic echinoderms, molluscs, and crustaceans (Wheeler 1985). The fusiform *M. ? smithsoni*, described earlier, also has a reinforced palate with a specialized dentition, suited for processing physically resilient prey. It is probably significant that two further members of the Bearsden fauna, the rhombic-bodied platysomid *Amphicentrum*, and the chimaeroid chondrichthyan *Deltoptychius* (Wood 1982; Dick *et al.* 1986) bear robust tooth-plates. However, we can only speculate, at present, upon the palaeoecological relationships between the specialized vertebrate predators and the diverse invertebrates (Wood 1982) of the Bearsden fauna.

Acknowledgements. The original research for this paper formed part of a thesis submitted for the degree of Ph.D. at the University of Newcastle upon Tyne, supervised by Dr A. L. Panchen, and funded by NERC. I am grateful to the following colleagues for helpful discussion and advice: Drs J. A. Long, K. A. Lowney, C. Patterson, N. D. L. Clark, T. R. Smithson, J. A. Clack and Professor B. G. Gardiner, and to Dr J. K. Ingham for permission to use his photographs. I thank Mr S. P. Wood, and the staffs of the Royal Museum of Scotland, Edinburgh; the Hunterian Museum, University of Glasgow; the Natural History Museum, London; the Hancock Museum, Newcastle-upon-Tyne; and the Scottish Geological Survey, Murchison House, for permission to examine and borrow specimens in their care. This paper is dedicated to the memory of Wilma Parkinson.

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Typescript received 9 September 1991

Revised typescript received 22 May 1992